

Studies on Distribution, Degree of Aerial Exposure, and Competitive Interactions in Four Species of Tropical Intertidal Gastropods

by

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Abstract. The vertical distributions of the limpet *Acmaea jamaicensis* and the littorines *Nodilittorina tuberculata*, *N. ziczac*, and *Littorina meleagris* were investigated on a vertical limestone block on the west coast of Barbados, W.I. Three vertical experimental plots and one vertical control plot were fenced off on the limestone block. In each of the experimental plots all gastropods except for one species of littorinid under study were removed. The control plot contained the natural density of all species of gastropods. Significant differences in distributional patterns were recorded between the experimental and control plots for all littorinid species after a 20-day period. When *L. meleagris* was living sympatrically with different experimental densities of *A. jamaicensis*, its distributional patterns were also shown to differ significantly, while reciprocal effects of *L. meleagris* on *A. jamaicensis* were not noted. Both sets of experimental data indicated the existence of interspecific competition among the four species of gastropods. In addition, variation among the three littorinids in functional morphology of the mantle cavity, and survival in air and water, were investigated, and the significance of these findings to the vertical distributional patterns of the four species was discussed.

INTRODUCTION

Species of littorinid snails are common inhabitants of upper intertidal and supratidal areas on many ocean shores. In this high intertidal-level position, conditions may be more terrestrial than marine, and the animals may spend considerable portions of their lives exposed to air, or perhaps wetted only from wave splash or spray. As a consequence, drying, exposure to damaging wavelengths of light, reduced feeding time, and possible heightened risk of predation may be important determinants of survival and distribution.

The means by which motile organisms position themselves at specific levels on the shore have commanded much attention over the past two decades, and gastropods have featured in a number of important studies of this topic (e.g., CONNELL, 1961, 1970; DAYTON, 1971; MENGE, 1976; LUBCHENKO & MENGE, 1978; GARRITY, 1984). Competition, as one specific mechanism involved in modifying and regulating community patterns in the intertidal area,

has been extensively investigated in gastropods (KOHN, 1959; HAVEN, 1973; STIMSON, 1973; BRANCH, 1975a, b, 1976; UNDERWOOD, 1976, 1978; BLACK, 1979; CREESE, 1982; CREESE & UNDERWOOD, 1982). However, while competitive interactions can be identified in gastropods and their effects often measured (by removing the competitive dominant), the actual function of competition in regulating patterns of distribution in intertidal snail populations is not clear. This has been emphasized by UNDERWOOD (1979) in his comprehensive review of the ecology of intertidal gastropods and, more recently, by CREESE (1982) and CREESE & UNDERWOOD (1982), who have shown that a competitively dominant species of grazing snail, while reducing the numbers or growth rates of other species of grazing snails, may not affect their patterns of distribution. Notwithstanding the observation by CHOAT (1977), that removal of the limpet *Collisella* (now *Lottia*) *digitalis* from its high-level intertidal position allowed another limpet *C. paradigitalis* (now *Lottia strigatella*; LINDBERG, 1986) to move to a higher than normal position, CREESE & UNDERWOOD (1982) suggest that no competitive interaction between any species of intertidal grazing gastropods has been demonstrated to determine limits of distribution,

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save for the special case of territorial limpets (e.g., as in the studies of SUTHERLAND [1970], STIMSON [1973], and BLACK [1979]).

In the present study we have investigated the possible role of competitive exclusion in defining distribution of three species of littorinid snails in Barbados, West Indies: *Nodilittorina tuberculata* Menke, 1928, *Nodilittorina* (*Nodilittorina*) *ziczac* (Gmelin, 1791), and *Littorina meleagris* Potiez & Michaud, 1838. *Nodilittorina tuberculata* is the numerically dominant of the three species, with a vertical distribution almost identical to that of *N. ziczac*. *Littorina meleagris* occurs at the lowest tidal level and is spatially separated from the other two littorinids, but its distribution overlaps almost completely that of the limpet *Acmaea jamaicensis* Gmelin, 1791. The biology of this limpet species is not well known. It appears to be a non-homing form, but with fairly strong "site-attachment" tendencies (i.e., its movements are limited). Because of its potential interaction with *L. meleagris*, it was included in certain of the studies on competition. In addition, we investigated the degree of aerial exposure, survival in air and water, and aspects of ctenidial morphology in relation to possibly differing modes of oxygen uptake in the three littorinid species.

Description of Habitat

The study site was located on the west coast of Barbados, West Indies, at Six Men's Bay (13°16'N, 59°38'W), 6.5 km north of the Bellairs Research Institute of McGill University. It consisted of an irregular beach-rock platform which was exposed at low tides and was occupied by a variety of snails, limpets, sea urchins, and algae. Two artificial berms, constructed of symmetrical limestone blocks, faced onto the beach-rock platform. Each provided a vertical intertidal surface measuring 2.1 m wide and 1.8 m high. The bases of the blocks were about 0.45 m above mean lower low water (MLLW). The faces of the blocks were completely exposed at most low tides, and were immersed to 1.2 m height and splashed to 2.0 m height on high monthly spring tides. Predominant gastropods on the vertical faces were the littorines *Nodilittorina tuberculata* (1.7 cm in length), *N. ziczac* (1.5 cm), and *Littorina meleagris* (0.5 cm), and the limpet *Acmaea jamaicensis* (1.3 cm). A variety of green algae and mixed diatoms formed a film over the vertical faces of the limestone blocks. Mean daily air temperature during the period of study (May–June) was 28–30°C; surface sea temperature was 28.5°C; and surface sea salinity was 32.0–33.0‰.

One limestone block provided the means to assess temporal changes in the distribution of each species of littorine with and without the presence of the other species of littorines. The other limestone block permitted study of the interactions between the low intertidal-inhabitants, the limpet *Acmaea jamaicensis* and the lowest-dwelling littorine *Littorina meleagris*. Preliminary observations showed that there was considerable overlap in the vertical distributions of the highest-dwelling species *Nodilittorina tuber-*

culata and *N. ziczac*, and some overlap of the lowest portion of the distribution of these species with that of the lowest-dwelling littorinid species *L. meleagris*, hence, providing potential for competition. Analysis of gut contents of all three species collected at high tide showed that similar foods were being eaten (see below) and the three species of littorines were also similar in their preferential occupation of depressions in the surface of the limestone; thus, competition could have been for either or both food and space.

Food Eaten

Six samples of epilithic algae were scraped from the experimental blocks using a stiff brush and fixed in 8% seawater-formalin. The samples were collected from six evenly spaced intertidal heights. Examination of the samples revealed that from 0–90 cm height in the blocks there was abundant growth of diatoms, algal sporelings, and other unicellular and filamentous species of green algae (0.45–1.35 m above MLLW), with a thicker-walled unicellular alga growing above 90 cm. Ten snails of each species were collected at high tide from the study site and preserved in 8% seawater-formalin in the field. Their stomach contents were compared to the algal samples and revealed that each species was grazing on the algal species occurring at its preferred vertical height. *Acmaea jamaicensis* and *Littorina meleagris* appeared to graze indiscriminately on algal flora occurring between 0–90 cm, and seemed to eat similar food items. *Nodilittorina tuberculata*, on the other hand, had a predominance of thick-walled unicellular algae representative of a higher intertidal position. *Nodilittorina ziczac*, though significantly overlapping the distribution of *N. tuberculata*, had more variable stomach contents indicating less selective grazing.

Competitive Interactions of Littorines

One limestone block was divided into four vertical plots, each being 50 cm in width and extending the entire intertidal height to about 20 cm above the high tide mark. Fences, constructed of 10-cm high aluminum mesh embedded in Z-SPAR epoxy putty, separated the plots and prevented animals from crossing from one to another. All snails, including limpets, were removed from three of the plots to leave one species only of littorinid snail in each of the plots; the fourth plot was left as a control. One day following this removal and thereafter at approximately 7-day intervals for 20 days, counts were made of individuals of all three littorinid species in 30-cm contiguous bands beginning from the lowest part of each plot (0 cm height in the block) and working upwards. Counts were made at both low tide and high tide (latter only from day 8–9) for each species. Temporal differences in distribution of a species in an experimental plot relative to its distribution in the control plot were analyzed using a Mann-Whitney U test. We hypothesized that if competitive in-

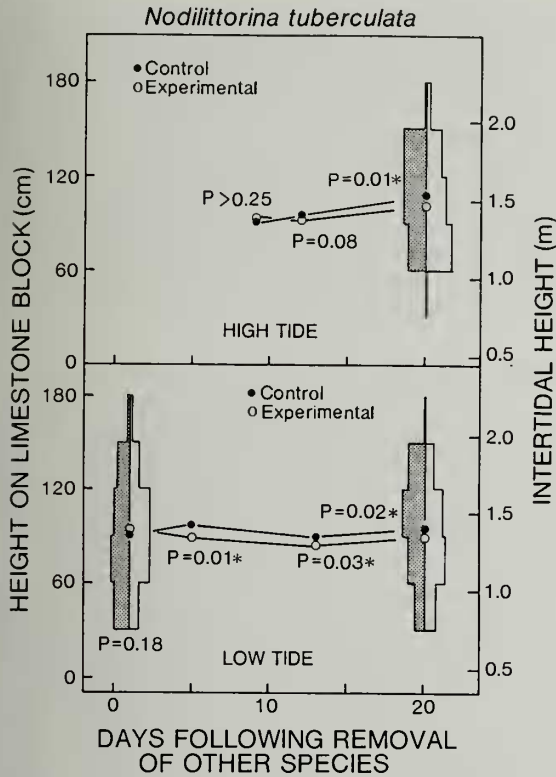


Figure 1

Temporal changes in distributional patterns of *Nodilittorina tuberculata* at high and low tides on limestone blocks in Barbados, W.I. The experimental animals occupied a plot where all other species of snails were removed. Their distribution is compared with the distribution of the same species in a control plot where all species were present. Each point represents the mean of 147–194 animals for the high-tide curves and 125–214 animals for the low-tide curves. Probability levels (one-tailed format) are determined from the Mann-Whitney U statistic calculated from the total distribution represented by each mean value. The histograms show distributions in bands of 30-cm height for each plot, expressed as percentages, for the starting and finishing days (control = closed circles, experimental = open circles). Width of each histogram indicates relative abundance.

interactions, possibly of the interference type, were restricting movements of the littorinid species, it would likely be downward for the uppermost species *Nodilittorina tuberculata*, upward for the lowermost species *Littorina meleagris*, and perhaps either way for the smaller of the uppermost species *N. ziczac*. Consequently, the analyses were one-tailed in the first two instances and two-tailed in the third. Because the distribution of a species in its experimental plot was compared simultaneously with its distribution in the control plot, any variation in distributional pattern due to environmental factors such as temperature, tidal exposure, or desiccation, assumed to affect a species alone or when in sympatry, would be taken into account.

Changes in distribution of each of the littorinid species in control and experimental plots over the 20-day exper-

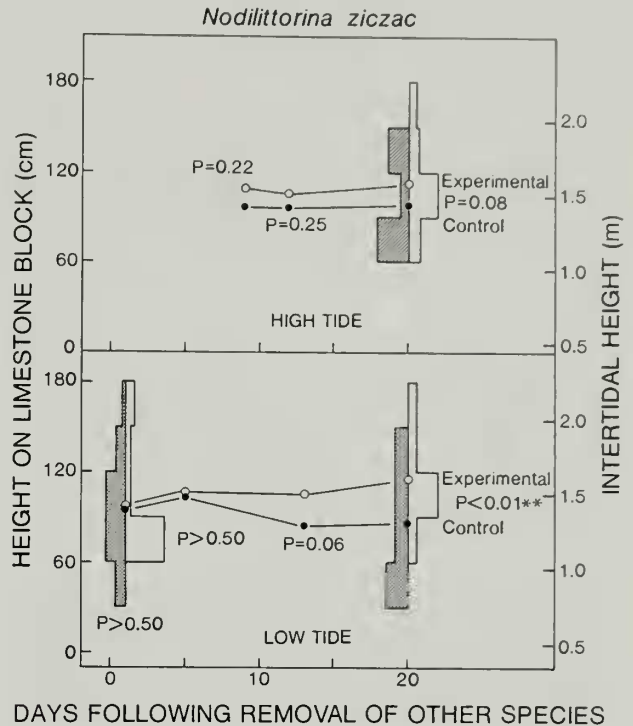


Figure 2

Temporal changes in distributional patterns of *Littorina ziczac* at high and low tides on limestone blocks in Barbados, W.I. Each point represents the mean of 20–32 animals for the high-tide curves and 19–35 animals for the low-tide curves. Probability levels (two-tailed format) are determined from the Mann-Whitney U statistic calculated from the total distribution represented by each mean value. Other details as specified for Figure 1.

imental period are shown at both high and low tides in Figures 1–3. Two major points are evident from these data. First, in the absence of the other gastropod species, the distribution of a given littorinid species changed significantly (all save for *Nodilittorina ziczac* at high tide). For two of the species the direction of movement was as predicted—namely, a movement of *N. tuberculata* downwards ($P = 0.01$ and 0.02 for comparisons of control and experimental distributions in each of high- and low-tide situations, respectively; Mann-Whitney U test), and a movement of *Littorina meleagris* upwards ($P < 0.001$ for comparisons of control and experimental distributions on day 20 in both high- and low-tide situations). The third species, *N. ziczac*, moved upwards in the absence of the other species of gastropods, although the day-20 difference between control and experimental distributions was only significantly different in the low-tide situation ($P < 0.01$), and not in the high-tide situation ($P = 0.08$). There was no evidence for a general broadening of distribution in the absence of potential competitors. This is shown by the general similarity of the histograms between day-1 and day-20 situations for a given species. The second major point to be noted from the data presented in Figures 1–3

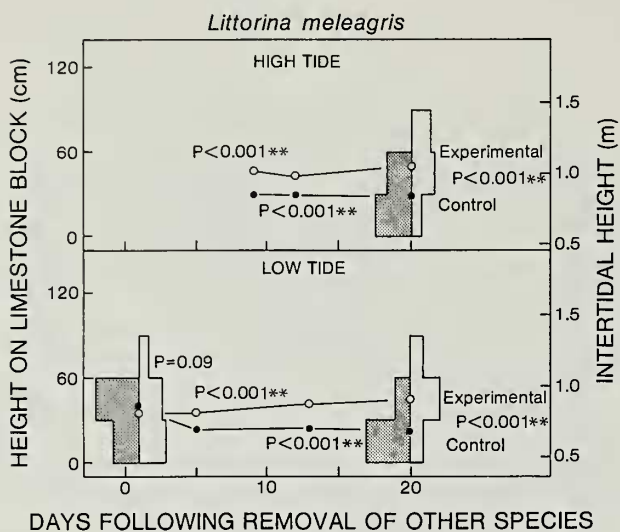


Figure 3

Temporal changes in distributional patterns of *Littorina meleagris* at high and low tides on limestone blocks in Barbados, W.I. Each point represents the mean of 70–159 animals for the high-tide curves and 54–184 animals for the low-tide curves. Probability levels (one-tailed format) are determined from the Mann-Whitney U statistic calculated from the total distribution represented by each mean value. Other details as specified for Figure 1.

is that, with some exceptions, the positions occupied by these littorinid species changed between high and low tides. Thus, in all instances save the *N. ziczac* experimental group (Figure 2) the animals moved upwards at high tide (considering the day-20 positions only; differences, however, were significant at $P = 0.05$ for only *N. tuberculata*, experimental and control groups, and *L. meleagris*, control group; Mann-Whitney U test). At the same time there appeared to be no discernible change in the pattern of

distribution of any of the littorinid species between spring- and neap-tide series. This may have been because the wave wash, extending almost the full height of the block (2.25 m above MLLW) on even moderate daily tides, would have obliterated such tidal effects. Change in abundance of a littorine species in response to absence of a possible competing species was not specifically investigated in this study. However, based on visual comparison of day-1 and day-20 histogram widths indicating numbers of littorines in 30-cm band heights for a given species (Figures 1–3), survivorship was good in all plots.

Limpet-Littorine Interactions

On the lowest part of the limestone blocks (0.45–1.00 m above MLLW) the distribution of the limpet *Acmaea jamaicensis* closely overlapped the distribution of the smallest littorine *Littorina meleagris*. Competitive interactions could include space, as both species preferentially occupied depressions in the limestone blocks, or food, or both.

To assess whether competitive interactions between *Acmaea jamaicensis* and *Littorina meleagris* were occurring, nearest-neighbor techniques were employed (CLARK & EVANS, 1954) in the following situations: (1) in the absence of limpets, (2) in the absence of littorines (only *L. meleagris* is present at this low-intertidal level), (3) where limpets were present in twice their original abundance, (4) where littorines were present in twice their original abundance, and (5) in a control area where each species was present in its original abundance. The nearest-neighbor method as employed here involved measuring distances from given individuals to their nearest-neighbors (conspecifics), and allowed the degree of aggregation or spacing of the population to be estimated.

The study was conducted on the second of the limestone blocks. Five areas of roughly 36×38 cm were delineated and each area separated from the next by a 2-cm wide

Table 1

Summary of nearest-neighbor data for populations of the limpet *Acmaea jamaicensis* and littorine *Littorina meleagris* under the control and experimental conditions shown. The statistic R is the ratio of mean nearest-neighbor distances observed, to mean nearest-neighbor distances expected, in an infinitely large random distribution. P indicates the probability of there being no difference between the observed spacing and randomness (F -test of variance ratios).

Condition	<i>Acmaea jamaicensis</i>				<i>Littorina meleagris</i>			
	Observed nearest-neighbor distances, \bar{x} cm	Theoretical expected nearest-neighbor distances, \bar{x} cm	R	P	Observed nearest-neighbor distances, \bar{x} cm	Theoretical expected nearest-neighbor distances, \bar{x} cm	R	P
Control	4.3	4.2	1.02	0.86	4.0	5.0	0.80	0.16
Limpets absent	—	—	—	—	3.1	5.3	0.58	<0.01
Littorines absent	3.0	3.3	0.91	0.36	—	—	—	—
Twice limpet density	2.8	2.6	1.08	0.52	4.0	4.6	0.87	0.36
Twice littorine density	3.5	3.7	0.95	0.70	2.1	3.6	0.58	<<0.001

border cleaned of all organisms. Plots were randomly assigned and densities adjusted based on numbers of each species present in the control plot. Some variation in numbers occurred in the 2-day period between the time of initial adjustment of densities and when the nearest-neighbor data were recorded. However, as no plot showed differences exceeding 15% of the assigned density over the two days, this variation was considered acceptable. The nearest-neighbor data were recorded at low tide from all animals in each plot. Measurements were taken from the apex of each limpet or from the center of the largest shell whorl of each littorine.

Table 1 gives the response of each species, measured as mean nearest-neighbor distances, to (1) the absence of the other species, (2) twice the original density of the other species, and (3) control conditions. The statistic R , the ratio of the mean nearest-neighbor distances observed to the mean nearest-neighbor distances expected in an infinitely large random distribution of a particular density, provides a measure of degree of aggregation (CLARK & EVANS, 1954). Where distributions are random, $R = 1$; where distributions are maximally aggregated, $R = 0$; and where distributions are maximally spaced, $R = 2.1491$. In the present study the limpets were distributed randomly in the control plot ($R = 1.02$, $P = 0.86$, F -test) and in all experimental plots (R values of 0.91, 1.08, and 0.95 under conditions where littorines were absent, where limpets were in twice their original density, and where littorines were in twice their original density, respectively). An ANOVA showed no significant differences between degree of spacing in these four limpet populations ($P > 0.50$). In contrast, the littorines responded to differences in density of the limpets by tending to disperse more widely under conditions of higher limpet-to-littorine densities (R values of 0.80 and 0.87 in the control plot and twice-limpet-density plot, respectively; these values, however, were not significantly different from random, $\alpha = 0.05$; see Table 1), and tending to aggregate more closely under conditions of lower limpet-to-littorine densities (R value of 0.58 for each of "limpets-absent" plot and "twice-littorine-density" plot; $P < 0.01$ and $\ll 0.001$, respectively). However, an ANOVA to test for differences in nearest-neighbor spacing in these four populations of littorines showed no significance ($P > 0.50$).

In summary, then, studies on intraspecific spacing in these limpet and littorine populations showed that the limpets were behaving independently of the littorines, while the littorines were tending to aggregate more when densities of limpets were lower, and tending to disperse more when densities of limpets were higher (noting that differences from randomness were not significant for the littorines).

Survival of Littorines in Air

Only one of the three littorinid species studied, *Littorina meleagris*, lives in the intertidal zone; the other two species

live in the supratidal area of the shore. Thus, in theory, while *L. meleagris* would be exposed to air some 90% of the time (as calculated from tidal charts for the 20-day study), the higher-dwelling species, *Nodilittorina tuberculata* and *N. ziczac*, would spend all of their time in air. In fact, wave action and spray wets all three species during most high tides. Only on extreme low tides, where the force of the waves is dissipated by the protective beachrock platform lying in front of the limestone blocks, would the three littorinid species be fully exposed to air.

Survival of the three species of littorines in dry air was measured by keeping animals in a 30-cm diameter desiccating flask over CaCl_2 and removing samples of each species at periodic intervals to test for recovery in seawater. For convenience in handling and to ensure that the snails did not clump together or change their orientation after placement in the flask, they were attached to standard glass microscope slides in sets of 10 of each species. Each animal was secured with plasticine at the largest shell whorl such that the snail was positioned with its aperture facing downwards onto the glass slide. The snails were arrayed on each slide in two evenly spaced rows of five. The size range of each species corresponded to average adult size, and snails were selected within as narrow a range as possible. The size ranges chosen were 11–13 mm (shell height) for *Nodilittorina tuberculata*, 10–12 mm for *N. ziczac*, and 5–6 mm for *Littorina meleagris*. Temperatures in the desiccator ranged from a maximum of 31°C during the day to a minimum of 26°C at night. Humidity was not measured, but was considered to be close to zero in the flask. At 3-day intervals (or slightly longer in a few instances) a microscope slide with its attached animals, one slide for each species, was removed from the flask. The animals were gently released from their mucus fastenings and placed in fresh seawater at room temperature (28°C). After 24 h the number of each species alive was recorded. When it was discovered that the lowermost intertidal species *L. meleagris* suffered almost 100% mortality in the first 3-day period, the procedure for this species was modified to test sets of animals at 8-h intervals over a 72-h period.

Figure 4 shows the percentage survival of each species in the desiccator flask. After 32 and 31 days the two supratidal species *Nodilittorina tuberculata* and *N. ziczac* had suffered about 25 and 75% mortality, respectively. In comparison, the lower-dwelling intertidal species *Littorina meleagris* had suffered almost 100% mortality in 3 days. The experiment was terminated after 32 days.

It should be noted that a second experiment, namely testing survival of fully immersed animals, produced no mortality in any of the three species over a 2-week period.

Comparative Ctenidial Morphology of the Three Littorinids

Initial observations of the mantle cavity of the three littorinids showed differences in the ctenidium structure which extends across the roof of the mantle cavity (Figure

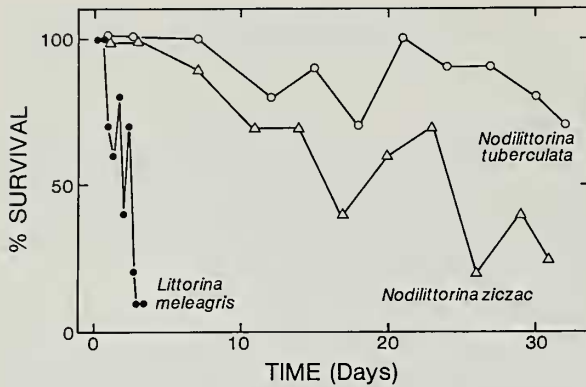


Figure 4

Percentage survival of *Nodilittorina tuberculata*, *N. ziczac*, and *Littorina meleagris* in dry air at 26–31°C. Each point represents the percentage of a set of 10 animals still alive after a 24-h recovery period in seawater.

5). Whole-mounts of individual ctenidial filaments taken from the broadest region of the ctenidium showed that in all three species there was a triangular region lateral to and left of the efferent branchial vessel where the epithelium consists of ciliated cells interspersed among cells exhibiting secretory activity (Figure 5). The latter are presumably mucus-producing cells, and this region of the ctenidium is thought to function in moving a water current across the surface of the ctenidium as well as in trapping and removing suspended matter entering the mantle cavity, as occurs in a wide variety of gastropods with aquatic gaseous exchange (FRETTER & GRAHAM, 1962). In *Littorina meleagris*, the entire ctenidium exhibits this cellular structure, while in *Nodilittorina ziczac* and *N. tuberculata*,

two regions can be distinguished in the ctenidium: a row of triangular filaments as described above (Figure 5) and, extending from this region, a row of sickle-shaped filaments spanning the mantle roof. The ventral surface of the latter region in both species is vascularized, and ciliated and secretory cells are absent. This part of the ctenidium is presumably important in aerial respiration.

To quantify these observed morphological differences, 21–23 specimens were selected from each species to include the entire size range of the population. These were anaesthetized in a 10% w/v solution of $MgCl_2$ in seawater for 24 h, then killed in the relaxed state by slow addition of 8% seawater-formalin solution to the narcotizing fluid. They were preserved in formalin, decalcified in a 10% solution of nitric acid, and then washed in three changes of distilled water. The ciliated and non-ciliated (if present) components of each ctenidium were carefully dissected out, and these two parts and the rest of the body were dried separately to constant weight at 80°C, and weighed.

The relationships between dry weights of the two ctenidial components and total shell-free dry body weight for the three species are shown in Figures 6 and 7. It is apparent that *Littorina meleagris* has the largest relative ciliated gill weight (dry weight of ciliated gill : dry weight of shell-free body) and thus, presumably, the greatest surface area of this component (here considered as an organ for aquatic gaseous exchange). Differences in relative ciliated gill weights and relative non-ciliated gill weights were tested between species pairs using a Mann-Whitney U test, with results shown in Table 2. From these results we conclude, (1) that *L. meleagris* differs from the other two littorinid species in having a significantly larger relative ciliated gill weight ($P < 0.001$ for comparisons of *L. meleagris* with each of the other two species; Table 2), (2)

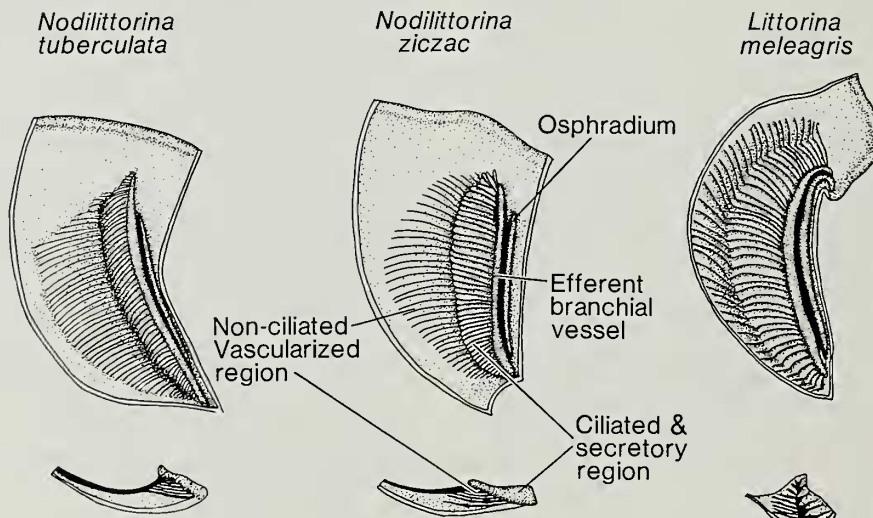


Figure 5

The morphology of the mantle roof of *Nodilittorina tuberculata*, *N. ziczac*, and *Littorina meleagris*, with detail of a ctenidial filament of each species taken from the broadest region of the ctenidium.

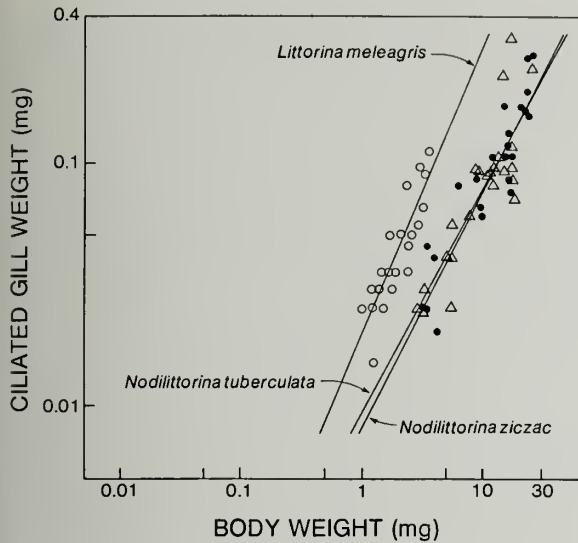


Figure 6

The relationship between ciliated gill dry weight and whole body dry weight in *Nodilittorina tuberculata* ($n = 23$, closed circle), *N. ziczac* ($n = 23$, triangle), and *Littorina meleagris* ($n = 21$, open circle). Equations of regressions, $\log Y = \log a + b \log X$: *N. tuberculata*: $\log a = -2.0365$, $b = 0.9372$, $r = 0.91$; *N. ziczac*: $\log a = -2.0930$, $b = 0.9736$, $r = 0.86$; *L. meleagris*: $\log a = -1.7104$, $b = 1.1799$, $r = 0.87$. All slopes are significantly different from 0 ($P < 0.001$).

that there are no significant differences between *Nodilittorina tuberculata* and *N. ziczac* with respect to the ciliated component of the ctenidium ($P > 0.50$), and (3) that *N. tuberculata* has a significantly larger relative non-ciliated gill weight compared to *N. ziczac* ($P < 0.001$).

DISCUSSION

Vertical distribution patterns of intertidal gastropods are regulated by a number of environmental factors. Interspecific competition, resistance or tolerance to desiccation and immersion, and morphological variation in relation to possible differential modes of gaseous exchange have been investigated in this study. We have assumed that in the absence of interspecific competition, each of the three littorinid species would occupy a "preferred" intertidal zone, the height and dimensions of which would be determined by other environmental constraints. Hence, any changes in distributional patterns resulting from removal of other littorinid species living in the same environment may have been indicative of interspecific competition.

Apart from the case of *Nodilittorina ziczac* at high tide, all experimental manipulations yielded significantly different distributional patterns in the littorines after a 20-day period. The observed differences occurring at low tide could imply that species were competing for shelter sites. Displacement at high tide, on the other hand, could imply that competition was arising from activities such as feeding, either through species interfering with one another during

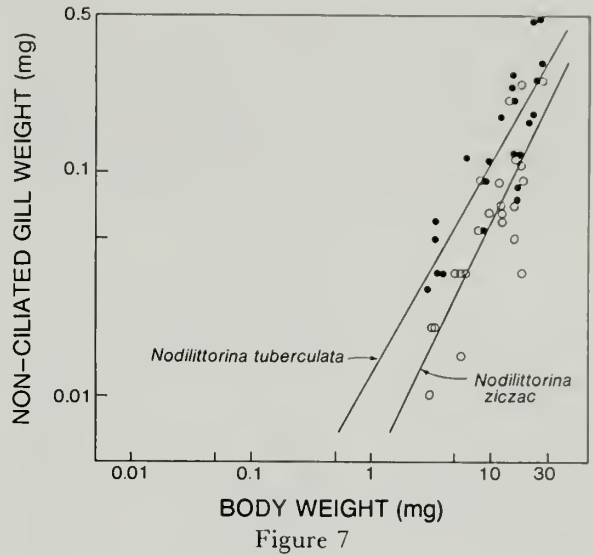


Figure 7

The relationship between non-ciliated gill dry weight and whole body dry weight in *Nodilittorina tuberculata* ($n = 23$, closed circle) and *N. ziczac* ($n = 23$, open circle). Equations for the regressions, $\log Y = \log a + b \log X$: *N. tuberculata*: $\log a = -1.9228$, $b = 0.9586$, $r = 0.84$; *N. ziczac*: $\log a = -2.3597$, $b = 1.1289$, $r = 0.83$. Both slopes are significantly different from 0 ($P < 0.001$).

foraging excursions or competing for actual food items. Removal experiments carried out on the limpet species-pairs *Collisella paradigitalis* (= *Lottia strigatella*) and *C. digitalis* (= *Lottia digitalis*) (CHOAT, 1977), and *C. digitalis* and "*Collisella*" *scabra* (HAVEN, 1973) resulted in displacement and differential growth rates, respectively, demonstrating in the first instance, at least, that similar competitive processes may have been occurring in these limpets as in our tropical littorines. In addition, our analyses of nearest-neighbor distances for *Littorina meleagris* and *Acmaea jamaicensis* suggested that the pattern of dispersion in the former species was responsive to manipulation of the densities of the latter.

While the present study has indicated possible effects of interspecific competition on distribution, the lack of replication in the experiments must be kept in mind. Position effects on the block, and possible fence effects and border interactions, could all have influenced the results. Also, little information is provided on the resource or resources for which the sympatric species may be competing. Additionally, while our experiments on the three littorinids demonstrate a displacement in vertical patterns of distribution, the effects of the manipulations on the dispersal of the species-pair *Acmaea jamaicensis* and *Littorina meleagris* indicate that other interactions may be occurring. In this regard, SCHOENER (1983) found the traditional classification of competition into "exploitative" and "interference" types unsatisfactory, and proposed a new division into six classes. Of these, "overgrowth" competition may be ignored in this study, as all species under investigation were motile. There was also no evidence of "chemical"

Table 2

Ratio of dry gill weight to dry body weight in the littorines *Nodilittorina tuberculata*, *N. ziczac*, and *Littorina meleagris*, with values of *Z* indicated for Mann-Whitney U tests on each species pair. Statistics for both ciliated and non-ciliated portions of the gills are shown.

Species	Dry gill weight: dry body weight	Z value (Mann-Whitney U test)	<i>P</i>
Ciliated			
<i>Nodilittorina tuberculata</i>	0.0083	5.52	>0.50
<i>N. ziczac</i>	0.0081		<0.001
<i>Littorina meleagris</i>	0.0227		<0.001
Non-ciliated			
<i>N. tuberculata</i>	0.0118	3.90	<0.001
<i>N. ziczac</i>	0.0065		

competition, as individuals of different species were observed to touch one another without any apparent escape or urticating reactions being elicited. There is a strong possibility that "preemptive" (passive occupation of space) and/or "consumptive" (consumption of a common food) competition may occur among the four species examined in this study, and the nearest-neighbor information obtained for *A. jamaicensis* and *L. meleagris* indicate the further possibility of "territorial" and "encounter" competition as defined by SCHOENER (1983). The basis for this conjecture is that while *A. jamaicensis* in high densities tended to increase intraspecific dispersal in *L. meleagris*, a reciprocal effect was not noted. Casual observations on 14 marked *A. jamaicensis* occupying identified resting sites at low tide indicated that 11 of them remained in the same position at low tide after a period of three days. This suggests that if these individuals had been foraging for food during that period, 79% had returned to a "home" site. Territorial defense of home ranges has been recorded for the acmaeid limpets "*Collisella*" *scabra* (SUTHERLAND, 1970) and *Lottia gigantea* (STIMSON, 1973) and for the pulmonate limpet *Siphonaria kurracheensis* (BLACK, 1979). A similar process in *A. jamaicensis* could account for the apparent random distribution of this species regardless of its own density, and for the unilateral influence of this species on *Littorina meleagris*, for which territorial behavior was not apparent.

While all four species under investigation were grazing on algae, some degree of specialization was apparent in *Nodilittorina tuberculata* which consumed mostly a thick-walled unicellular alga inhabiting the high intertidal levels. There was no further evidence of food partitioning among the four species. Thus, had food become a limiting factor, competition should have occurred. The shift in distributional patterns occurring between experimental and con-

trol snails at high tide unfortunately provides no direct evidence for either an interference type of competition, perhaps during feeding excursions, or an exploitative type of competition for common food resources.

While competitive effects were demonstrated amongst these four species of gastropods, changes in vertical distribution following the removal of competitively dominant species were not as large as might be predicted on the basis of the amount of space made available ("preemptive" competition), and presumably food made available ("consumptive" competition). Thus, in the absence of competitors, neither species of *Nodilittorina* descended to the lowest level of the experimental block, despite the greater variety of food there. Furthermore, *Littorina meleagris* only moved upwards 30 cm in the absence of the other species and thus did not occupy all the available space. Our findings apparently contrast those of DAYTON (1971), MENGE (1976), and others in studies of temperate rocky shores where space has been demonstrated to be a limited resource.

Predation has been shown to influence the lower limits and patterns of distribution in a number of intertidal species (CONNELL, 1961; PAINE, 1971, 1974; LUBCHENCO & MENGE, 1978; MENGE, 1976; GARRITY & LEVINGS, 1981) and the possibility that *Nodilittorina tuberculata* and *N. ziczac* were similarly regulated cannot be ignored. In this regard, HAMILTON (1976) suggested that upshore migration of *Littorina irrorata* was an escape reaction to predation by the portunid crab *Callinectes sapidus*, and MCQUAID (1982) proposed that the gastropod *Oxysteles variegata* migrated upshore to the degree that its tolerance to aerial exposure would allow as an escape response to predation by the whelk *Burnupena delalandii*. In the Six Men's Bay study area, species closely related to those commonly identified as predators of *Littorina* spp. (see PETTITT, 1975) were either not present or occurred only sporadically. For example, three species of *Thais* (Muricidae) recorded in LEWIS' (1960) faunal description of western Barbados coasts were rarely encountered. Although predation by fishes at high tide was a strong possibility (McCORMACK, 1982), the dominant presence of *L. meleagris*, a much smaller and softer-shelled species, in the lowest intertidal level of the experimental block provided circumstantial evidence that predation by fish at high tide was unlikely to be of major importance. Furthermore, the downward migration of *N. tuberculata* after experimental manipulation did not result in a significant progressive reduction in numbers within the total plot area throughout the course of the experimental period, which was to be expected if downward migration resulted in increased susceptibility to predation at high tide.

The apparent avoidance by *Nodilittorina tuberculata* of low intertidal regions may have been related to a preference for unicellular algae (comparatively less abundant in the lower intertidal regions) or to a greater reliance by this species on an aerial mode of oxygen uptake. Examination of the mantle cavity revealed that both of the higher level

species *N. tuberculata* and *N. ziczac* had two components making up the ctenidium, apparently adapted to each of aerial and aquatic gaseous exchange, respectively (Figure 5). (In comparison, the lowermost species *Littorina meleagris* lacked the non-ciliated or aerial portion of the gill entirely.) This morphological development may have limited the degree of aquatic gaseous exchange in these uppermost species, leading to an avoidance of lower shore levels and the associated long periods of immersion. Although periods of immersion of 14 days did not result in death in any of the species, the condition of the animals was not monitored. Further research would be needed to examine the degree of differential reliance on aerial and aquatic respiration in these littorinid species.

Our investigation on zonation patterns of the three species of littorinids accords with BANDEL's observations (1974) on the same species from a number of sites in the Atlantic. This consistency in zonation pattern, together with data presented here showing an increased tolerance to desiccation, as well as a tendency for morphological modifications in the mantle cavity in those species occupying high intertidal levels, indicate that physical stresses associated with aerial exposure may limit upper distribution. VERMEIJ (1973) also found morphological gradients in increased shell sculpture and relative spire height among intertidal tropical littorinids as intertidal heights increased, and considered that these features increased the snails' tolerance to water loss and heat stress associated with their high intertidal life. However, if as WOLCOTT (1973) has hypothesized, intertidal gastropods are invariably zoned just below the limits of their tolerance to various environmental factors, then deaths resulting from such stresses that act to limit upper distributions of a species may occur only rarely. Each of the three littorinids tested in the present study showed tolerance to desiccating circumstances that exceeded the tolerance required for survival in the uppermost region of their distribution. Thus, wave splash on the experimental block would ensure that *Littorina meleagris* would experience exposure to air for only brief periods during each tide, while both species of *Nodilittorina* would experience wetting at least during spring tides, the intervals between these being considerably shorter than that required to achieve significant mortality in the laboratory experiment (Figure 4). While these results offer some support to the notion that desiccation may be setting upper limits of distribution of these tropical littorinids, especially for *L. meleagris*, we must heed UNDERWOOD's (1979) caution that field experiments are necessary to establish firmly the critical limits of tolerance of a species to physical stresses.

Much information is currently available on the structuring of intertidal communities on temperate shores, particularly on the interplay between the relative importance of physical factors and various biological factors, such as predation and competition (e.g., DAYTON, 1971; CONNELL, 1961, 1975; MENGE, 1976; BLACK, 1979). However, there are fewer comparable reports on tropical littoral systems,

especially with regard to long-term studies on competition (see LEVINGS & GARRITY, 1983). Owing to significant differences in physical and biological properties between temperate and tropical systems (see BRANCH, 1976; GARRITY, 1984), generalizations made on the basis of studies in one may not apply to the other, and more research will be needed to unravel the role that competition plays in the structuring of intertidal systems in the tropics.

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LITERATURE CITED

- BANDEL, K. 1974. Studies on Littorinidae from the Atlantic. *Veliger* 17:92-114.
- BLACK, R. 1979. Competition between intertidal limpets: an intrusive niche on a steep resource gradient. *Jour. Anim. Ecol.* 48:401-411.
- BRANCH, G. M. 1975a. Intraspecific competition in *Patella cochlear* Born. *Jour. Anim. Ecol.* 44:263-281.
- BRANCH, G. M. 1975b. Mechanisms reducing intraspecific competition in *Patella* spp.: migration, differentiation and territorial behaviour. *Jour. Anim. Ecol.* 44:575-600.
- BRANCH, G. M. 1976. Interspecific competition experienced by South African *Patella* species. *Jour. Anim. Ecol.* 45:507-529.
- CHOAT, J. H. 1977. The influence of sessile organisms on the population biology of three species of acmaeid limpets. *Jour. Exp. Mar. Biol. Ecol.* 26:1-26.
- CLARK, P. J. & F. C. EVANS. 1954. Distance to nearest neighbour as a measure of spatial relationships in populations. *Ecology* 35:445-453.
- CONNELL, J. H. 1961. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. *Ecol. Monogr.* 31:61-104.
- CONNELL, J. H. 1970. A predator-prey system in the marine intertidal region. I. *Balanus glandula* and several predatory species of *Thais*. *Ecol. Monogr.* 40:49-78.
- CONNELL, J. H. 1975. Some mechanisms producing structure in natural communities: a model and evidence from field experiments. Pp. 460-490. *In*: M. L. Cody and J. M. Diamond (eds.), *Ecology and evolution of communities*. Harvard University Press: Cambridge, Massachusetts.
- CREESE, R. G. 1982. Distribution and abundance of the acmaeid limpet, *Patelloida latistrigata*. *Oecologia* 52:85-96.
- CREESE, R. G. & A. J. UNDERWOOD. 1982. Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. *Oecologia* 53:337-346.
- DAYTON, P. K. 1971. Competition, disturbance, and community organization: the provision and subsequent utilization

- of space in a rocky intertidal community. *Ecol. Monogr.* 41: 351-389.
- FRETTER, V. & A. GRAHAM. 1962. British prosobranch molluscs. Ray Society: London. 755 pp.
- GARRITY, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* 65:559-574.
- GARRITY, S. D. & S. C. LEVINGS. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. *Ecol. Monogr.* 51:267-286.
- HAMILTON, P. V. 1976. Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). *Bull. Mar. Sci.* 26:403-409.
- HAVEN, S. B. 1973. Competition for food between the intertidal gastropods *Acmaea scabra* and *Acmaea digitalis*. *Ecology* 54: 143-151.
- KOHN, A. J. 1959. The ecology of *Conus* in Hawaii. *Ecol. Monogr.* 29:47-90.
- LEVINGS, S. C. & S. D. GARRITY. 1983. Diel and tidal movement of two co-occurring neritid snails; differences in grazing patterns on a tropical rocky shore. *Jour. Exp. Mar. Biol. Ecol.* 67:261-278.
- LEWIS, J. B. 1960. The fauna of rocky shores of Barbados, West Indies. *Can. Jour. Zool.* 38:391-435.
- LINDBERG, D. R. 1986. Name changes in the "Acmaeidae." *Veliger* 29:142-148.
- LUBCHENCO, J. & B. A. MENGE. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.* 48:67-94.
- MCCORMACK, S. M. D. 1982. The maintenance of shore-level size gradients in an intertidal snail (*Littorina sithkana*). *Oecologia* 54:177-183.
- MCQUAID, C. D. 1982. The influence of desiccation and predation on vertical size gradients in populations of the gastropod *Oxysteles variegata* (Anton) on an exposed rocky shore. *Oecologia* 53:123-127.
- MENGE, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.* 46:355-393.
- PAINE, R. T. 1971. A short-term experimental investigation of resource partitioning in a New Zealand rocky intertidal habitat. *Ecology* 52:1096-1106.
- PAINE, R. T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* 15:93-120.
- PETTITT, C. 1975. A review of the predators of *Littorina*, especially those of *L. saxatilis* (Oliv) (Gastropoda: Prosobranchia). *Jour. Conch.* 28:343-357.
- SCHOENER, T. W. 1983. Field experiments on interspecific competition. *Amer. Natur.* 122:240-285.
- STIMSON, J. 1973. The role of the territory in the ecology of the intertidal limpet *Lottia gigantea* (Gray). *Ecology* 54:1020-1030.
- SUTHERLAND, J. P. 1970. Dynamics of high and low populations of the limpet, *Acmaea scabra* (Gould). *Ecol. Monogr.* 40:169-188.
- UNDERWOOD, A. J. 1976. Food competition between age-classes in the intertidal neritacean *Nerita atramentosa* Reeve (Gastropoda: Prosobranchia). *Jour. Exp. Mar. Biol. Ecol.* 23: 145-154.
- UNDERWOOD, A. J. 1978. An experimental evaluation of competition between three species of intertidal prosobranch gastropods. *Oecologia* 33:185-202.
- UNDERWOOD, A. J. 1979. The ecology of intertidal gastropods. *Adv. Mar. Biol.* 16:111-210.
- VERMEIJ, G. J. 1973. Morphological patterns in high-intertidal gastropods: adaptive strategies and their limitations. *Mar. Biol.* 20:319-346.
- WOLCOTT, T. G. 1973. Physiological ecology and intertidal zonation in limpets (*Acmaea*): a critical look at "limiting factors." *Biol. Bull.* 145:389-422.